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Phenotypic responses of lacustrine brook charr in relation to the intensity of interspecific competition

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Abstract. We investigated the structure of interindividual variations in the diet of brook charr (*Salvelinus fontinalis*) based on stomach contents data of 3776 charr captured in 69 lakes of the Canadian Shield (Québec, Canada); 29 of these contained allopatric brook charr populations, 24 contained brook charr and creek chub (*Semotilus atromaculatus*) and 16 contained brook charr and white sucker (*Catostomus commersoni*). In any given lake, some of the charr fed almost exclusively on benthic organisms ('benthic specialists', i.e., mean percent weight of benthic prey >90%), others, almost exclusively on pelagic prey ('pelagic specialists', i.e., mean percent weight of benthic prey <10%), and a lesser proportion were 'generalist feeders' (i.e. mean percent weight of benthic prey between 10 and 90%). The proportion of benthic and pelagic specialists were respectively 41.3 and 18% in allopatric brook charr populations. These proportions fit remarkably well with those based on interindividual preferences in spatial distribution, identified through radio-telemetry in another study done in two lakes of the same area. The proportion of benthic specialists was related to competition for benthic organisms with creek chub and white sucker. The effect of white sucker on brook charr diet was more pronounced than that of creek chub: the proportion of benthic specialists among brook charr decreased from 41.3% in allopatry to 19.7% in sympatry with creek chub, and to 9.9% in sympatry with white sucker. Other response variables of brook charr populations also indicate that white sucker is a stronger competitor than creek chub in this system. Because sucker and chub were introduced in these lakes during the last century, phenotypic responses of brook charr to interspecific competition appear to be rapid. Furthermore, in addition to providing a strong field support to the current hypothesis that polymorphism is promoted by arelaxation of interspecific competition, our results also indicate that phenotypic response of brook charr (i.e. the proportion of each form in a given lake) is related to the intensity of this competition.

Key words: *Catostomus commersoni*, diet, interindividual variations, interspecific competition, intraspecific competition, phenotypic responses, *Salvelinus fontinalis*, *Semotilus atromaculatus*, trophic polymorphism

Introduction

Recent reviews have shown that trophic polymorphisms are common among vertebrates (Robinson and Wilson, 1994; Wimberger, 1994; Skulason and Smith, 1995). Such trophic diversification among individuals of the same species seems to be more the rule than the exception in fish inhabiting speciespoor lakes of the northern hemisphere; these lakes offer basically two functional habitats, the littoral and pelagic zones, and studies reporting on trophic polymorphisms almost always include coexisting benthic and pelagic forms (Robinson and Wilson, 1994). There are essentially two kinds of trophic polymorphism in fishes; one involves sharp differences between forms (or morphs), while the other is much more subtle and for this reason is probably often overlooked. The best known example of sharp polymorphisms is the case of landlocked Arctic charr (*Salvelinus alpinus*) in which four coexisting morphs differ clearly in morphology, habitat selection, diet, and behavior: large benthivorous, small benthivorous, planktivorous, and piscivorous charr (Sandlun *et al*., 1987; Jonsson *et al*., 1988; Snorrason *et al*., 1989; Malmquist *et al*., 1992; Skulason *et al*., 1993). On the other hand, in the absence of bluegill sunfish (*Lepomis macrochirus*) pumpkinseed sunfish (*Lepomis gibbosus*) can be trophically polymorphic, with a planktivorous and a benthic form (Ehlinger and Wilson, 1988; Robinson *et al*., 1993). In the latter example, the differences, in body form and gill raker structure, are much more subtle and can only be detected with multivariate analyses.

Whether they are subtle or sharp, intraspecific differences in morphology and behavior of individuals appear to be adaptive because there is evidence that, within a population, each form is better adapted than the other(s) to forage in its own niche (e.g. benthic form in the littoral zone versus planktivorous form in the pelagic zone; Snorrason *et al*., 1989; Ehlinger, 1990; Skulason *et al*., 1993; Robinson *et al*., 1993; Robinson and Wilson, 1994; Schluter, 1994, 1995; Skulason and Smith, 1995). It is hypothesized that trophic polymorphism is promoted by the presence of an 'empty' niche, either by a relaxation of interspecific competition or in response to intraspecific competition (Robinson and Wilson, 1994; Skulason and Smith, 1995). By extension, one can predict that variation in the *intensity* of competition (either intra- or interspecific) will affect not only the occurrence, but also the abundance of the different forms in fish populations. Despite the existence of some circumstantial evidence supporting the latter hypothesis (Skulason and Smith, 1995) we do not know of any empirical data from the same system providing stronger support.

Bourke *et al*. (1997) observed that brook charr (*Salvelinus fontinalis*) exhibit interindividual differences in habitat use in two Canadian Shield lakes; 50% of 28 radio-tracked fish were found mainly in the benthic zone, 18% in the pelagic zone, and 32% travelled regularly between the two zones. Interindividual differences in habitat preference were related to functional differences in body morphology and coloration; the pectoral fins of benthic and generalist individuals were significantly longer than those of pelagic ones and the coloration of the lower flank of benthic and generalist individuals was silver-grey, while that of pelagic individuals was red (Bourke *et al*., 1997). These results suggest that brook charr inhabiting these lakes exhibit a subtle trophic polymorphism, where some individuals are specialists better adapted to feeding in the littoral zone whereas others are specialists better adapted to feeding in the pelagic zone. In the present study, we carried out a new analysis on our charr data base (see Data base section below) to (1) determine if the pattern of interindividual variations in the diet of brook charr is related to the pattern of interindividual variations in habitat use observed by Bourke *et al.* (1997) in allopatric lakes, and if so (2) test the hypothesis that phenotypic response of brook charr (i.e. the proportion of each form in a given lake, based on diet data) is related to the *intensity* of interspecific competition. In this system, different response variables of brook charr populations indicate that white sucker (*Catostomus commersoni*) is a stronger competitor than creek chub (*Semotilus atromaculatus*) (see section below).

Biological background

Brook charr are found in sympatry with creek chub and white sucker in many oligotrophic lakes of southern Québec, Canada. Cyprinids and catostomids were introduced in these lakes by bait fishers during the last century, or colonized these habitats after natural barriers disappeared due to logging practices early this century (Bilby and Ward, 1991; Lacasse and Magnan, 1992). Brook charr colonized the area following the last glaciation (Lacasse and Magnan, 1994). These lakes are typical of small, oligotrophic temperate zone lakes, with respect to surface area, mean depth, conductivity, Secchi disk transparency, thermal stratification, and oxygen concentration (Magnan, 1988, 1989; Lacasse and Magnan, 1992) and located within a 3000 km^2 area.

The impact of introduced species on brook charr populations has been investigated since 1978 in this study area, mainly by comparing allopatric brook charr to populations living sympatrically with introduced species. Comparisons were made on replicates of allopatric and sympatric brook charr populations. The presence of competing species involves significant reductions in the mean production of brook charr, as determined by sport fishing (kg per hectare per year; Magnan 1988, Magnan *et al.*, 1999) and gill net fishing (catch per unit of effort; Magnan *et al.*, 1999). The presence of chub and sucker is also related with a shift in diet and spatial distribution of charr from benthic invertebrates of the littoral zone, in allopatry, to zooplankton and open water prey of the pelagic zone, in sympatry (Magnan and FitzGerald, 1982; Magnan, 1988; Lachance and Magnan, 1990; Tremblay and Magnan, 1991; East and Magnan, 1991; Lacasse and Magnan, 1992). The shift to zooplankton and open water prey in sympatry is related with significant increase in the length of gill rakers and change in pyloric caecal morphology of charr (Magnan, 1988; Magnan and Stevens, 1993), with consistent changes in their parasite fauna (Dubois *et al.*, 1996; Bergeron *et al.*, 1997), and with significant changes in the structure of the zooplankton community (Magnan, 1988; Rodríguez *et al.*, 1993). Creek chub and white sucker, which feed mostly on benthic invertebrates, appear to be better adapted (morphologically and behaviorally) than brook charr to feeding on bottom prey (Magnan and FitzGerald, 1984; Magnan, 1988; Tremblay and Magnan, 1991). For all the above response variables, we have found that the intensity of interspecific competition increases sequentially from allopatric brook charr populations (no interspecific competition), to brook charr and creek chub populations (intermediate interspecific competition), and to brook charr and white sucker populations (highest interspecific competition). This system thus provides a good model to investigate how the intensity of competition is related to phenotypic responses of a fish species, over a relatively short time scale (as chub and sucker were introduced recently in this system).

Materials and methods

Data base

The present study is based on stomach content analyses of 3776 brook charr captured in 69 lakes located in the Mastigouche and St. Maurice reserves, Québec, Canada. Data on diets as well as fish communities of the study lakes were obtained from seven studies done previously in this system (Magnan, 1988; Lachance and Magnan, 1990; Tremblay and Magnan, 1991; East and Magnan, 1991; Lacasse and Magnan, 1992; Venne and Magnan, 1995; Lapointe and Magnan, unpublished data). These studies mainly evaluated the impact of white sucker and creek chub on the diet of brook charr populations. The relative contribution of the spatial structure and environmental variables on the diet of charr also has been evaluated in this system (Lacasse and Magnan, 1992; Magnan *et al.*, 1994). These earlier studies analysed the 'mean response' of the populations based on the mean percent weight of different prey categories (Hyslop, 1980). In the present study, we address questions about interindividual dietary variations instead.

Study lakes

The study lakes ranged from 3.9 to 500.8 ha in surface area, and from 2.5 to 17.6 m in mean depth. Of the 69 study lakes, 29 contained allopatric brook charr populations (no interspecific competition), 24 contained brook charr and creek chub (intermediate interspecific competition), and 16 contained brook charr and white sucker (highest interspecific competition). We hereafter refer to these as 'brook charr lakes', 'brook charr and creek chub lakes', and 'brook charr and white sucker lakes', respectively. Northern redbelly dace (*Phoxinus* *eos*) was present in almost all lakes but its presence did not significantly affect the mean yield of brook charr in the exploited lakes of the St. Maurice and Mastigouche reserves (Magnan, unpublished data). Creek chub and pearl dace (*Margariscus margarita*) were also present in some of the brook charr and white sucker lakes, but gillnet fishing in three of these lakes indicated that their relative biomass represented less than 1% of the total fish biomass (Magnan, unpublished data). All lakes were subject to sportfishing, and exploitation was carefully controlled by the Québec government.

Stomach samples

A mean of 20 stomachs per lake and date was collected from brook charr captured by angling (sport fishers) or by gillnet fishing, depending on the study. Sport fishers were given a cooler in which they could retain captured brook charr without eviscerating them. Upon the angler's return, or immediately after capture (gillnet fishing), the total length of each brook charr was recorded and its stomach was removed and preserved in a 10% formaldehyde solution. In the laboratory, the weight of different prey categories was estimated as dry weight (±0.01 mg) of prey identified to order or family in Tremblay and Magnan (1991), Lachance and Magnan (1990), Venne and Magnan (1995), and Lapointe and Magnan (unpublished); and wet weight (±0.01 mg) of the following prey categories in Magnan (1988), East and Magnan (1991), and Lacasse and Magnan (1992): zoobenthos, amphipods, zooplankton, dipteran pupae, swimming insects, terrestrial insects, and prey-fish.

Statistical analysis

To describe the structure of interindividual variation in the diet of brook charr, we plotted the frequency of individuals against the percent weight of benthic organisms found in their stomach (the preferred prey of brook charr in allopatry; see references above). As the charr feed mainly in two habitats, the littoral zone (on benthic prey) and the pelagic zone (on zooplankton, dipteran pupae, swimming insects, terrestrial insects, and prey fish), we do not present these plots for pelagic prey because they always represent the complement of the percent weight of benthic prey (Bourke, 1996).

Stepwise multiple regressions were used to determine if the proportion of individuals having more than 90% of benthic prey in their stomach is significantly related to the presence of creek chub and white sucker after adjusting statistically for the effects of environmental variables (physical and chemical properties, littoral habitat structure; Lacasse and Magnan, 1992). The proportion of individuals having more than 90% of benthic prey in their stomach (dependent variable) was transformed as arcsin sqr(p). Among the independent variables, the presence of creek chub and white sucker was coded with two binary (0, 1) dummy variables; environmental variables were transformed whenever necessary to meet statistical assumptions. The analyses were performed with the SPSS X.2 regression procedure which uses the 'tolerance and minimum tolerance tests' to prevent collinearity problems (Tabachnick and Fidell, 1983). One regression model was built for each data set (see Data base section above).

Results and discussion

Although analyses on frequency distributions were done for each data set separately, only those for pooled samples are presented because the patterns were similar among data sets (see Bourke (1996) for presentation of separate samples). The results show great within-population variability in the diet of brook charr (Fig. 1). Some of the charr had fed almost exclusively on benthic organisms (mean percent weight of benthic prey $>90\%$; benthic specialists), others, almost exclusively on pelagic prey (mean percent weight of benthic prey $<10\%$; pelagic specialists), and the rest were 'generalists' (mean percent weight of benthic prey between 10% and 90%). These results indicate that charr populations in the study lakes were not composed by an ensemble of generalist individuals with regard to feeding habits, as usually suggested (Scott and Crossman, 1977; Power, 1980), but rather by a combination of benthic and pelagic specialists in varying proportions, with a lesser contribution by generalists. If we consider that fish having $>90\%$ of a given prey type in their stomach are specialists on this prey type, the proportion of benthic and pelagic specialists are respectively 41.3% and 18% in allopatric brook charr lakes (sum of the two rightmost and two leftmost bars on Figure 1 respectively). These results fit remarkably well with those of Bourke *et al.* (1997), who studied interindividual variations in habitat preference of allopatric brook charr in two lakes of the same system using radio-telemetry and found that 50% of the 28 tracked brook charr were benthic specialists, 18% pelagic specialists, and 32% generalists. This correspondence between the two data sets suggests that the pattern of interindividual variations in diet is representative of the long-term interindividual preferences in habitat use in allopatric brook charr, at least in the present study (stomach contents from a large number of individuals, coming from many different lakes, sampling dates and years). Thus, it seems reasonable to estimate the proportion of benthic and pelagic specialists among communities from data on interindividual variations in diet.

The analysis of stomach content data also showed considerable interindividual variation in the diet of brook charr among fish communities (i.e. brook charr, brook charr and creek chub, and brook charr and white sucker lakes; Fig. 1); the proportion of benthic specialists (mean percent weight of benthic prey $>90\%$) decreased from 41.3% in allopatry to 19.7% in sympatry with

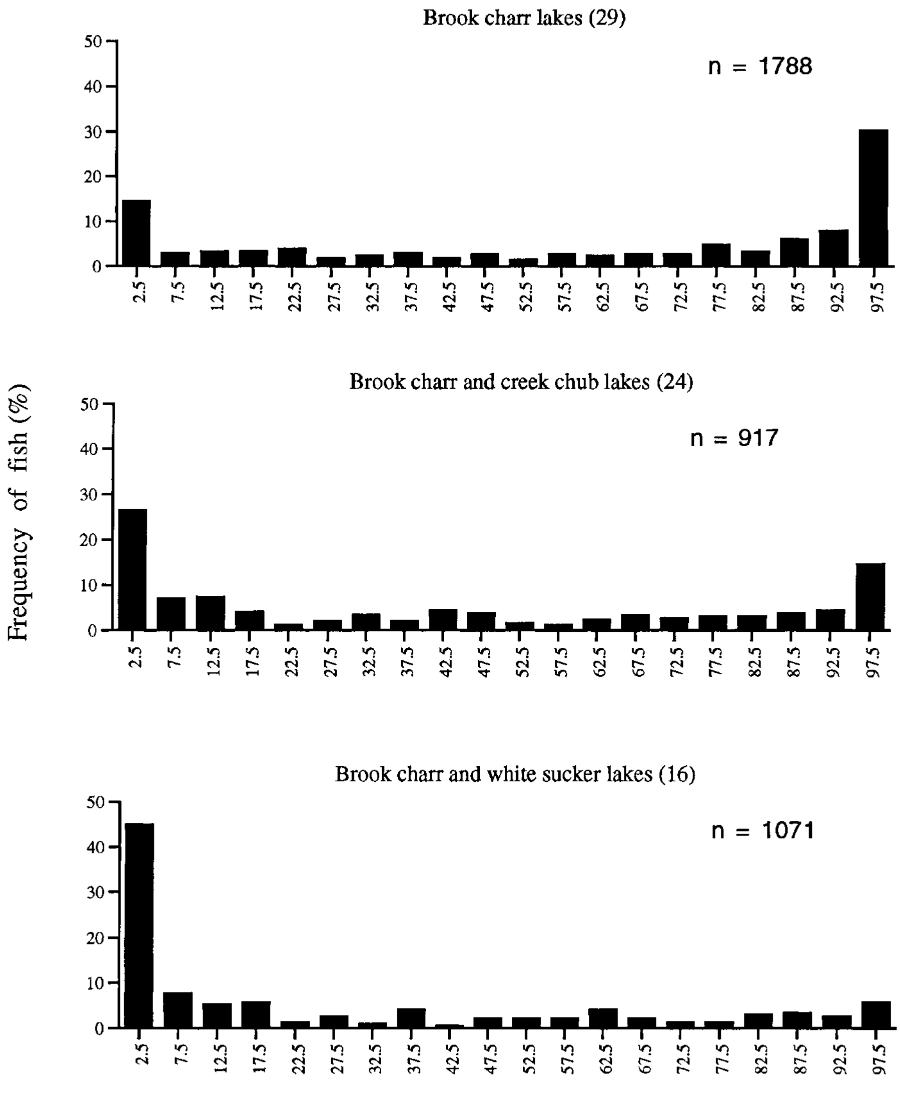

Figure 1. Frequency of individuals in relation to the percentage of benthic prey in their stomach for brook charr lakes, brook charr and creek chub lakes, and brook charr and white sucker lakes. The number of stomach contents analysed appears at the top of each figure and the number of lakes, in parentheses.

creek chub, and to 9.9% in sympatry with white sucker. It is remarkable that the proportion of generalist individuals was virtually the same among the fish communities (Fig. 1). In this context, the niche shift of sympatric brook charr from benthic organisms to pelagic prey is not the result of increased consumption of pelagic prey by most individuals of the population (i.e. an increase in the proportion of individuals behaving as generalists), but rather of a decrease in the proportion of benthic specialists relative to that of pelagic specialists (Fig. 1). The presence of white sucker (partial $r^2 = 28.5 - 37.9$ depending on the data set, $p < 0.05 - 0.001$) and to a lesser extent that of creek chub (partial $r^2 = 25.7$, $p < 0.01$) were negatively related with the proportion of benthic specialists.

These results are thus consistent with the observation that white sucker have a greater impact than creek chub on brook charr populations (see Biological background section) and they suggest that the proportions of benthic and littoral forms are related to the intensity of competition. It was suggested earlier that sympatric brook charr shift to pelagic prey because chub and sucker are morphologically and behaviourally better adapted than charr to feed on bottom prey (Magnan, 1988, 1989; Tremblay and Magnan, 1991); the feeding apparatus of creek chub (mouth in subterminal position and protrusible premaxillae) and white sucker (mouth protrusible and in inferior position) should allow them to use bottom prey more efficiently than brook charr, which have a terminal mouth. Generally, fish with a bottom-oriented mouth, or with adaptations permitting to orient the mouth downward (such as protrusible premaxillae), are more efficient when feeding on benthic prey, while fish with terminal mouths are more efficient at capturing surface and mid-water prey (Schultz and Northcote, 1972; Gatz, 1979; McComas and Drenner, 1982; Paine *et al.*, 1982; Webb, 1984). In term of feeding behavior, creek chub and white sucker are better able than brook charr to exploit hidden and patchy benthic prey. For creek chub, laboratory experiments have shown that searching efficiency of an individual feeding in a group is improved through social facilitation (Magnan and FitzGerald, 1984). Such a feeding strategy would be advantageous for species that feed on patchy, widely dispersed, and unpredictable food resources (Morse, 1977; Bertram, 1978), such as benthic invertebrates in temperate lakes (Wetzel, 1983). In contrast, the high level of intraspecific aggression observed in brook charr prevents the formation of such feeding groups (Magnan and FitzGerald, 1984; East and Magnan, 1987). Also, the size distribution of benthic prey consumed by white sucker is similar to that of benthic invertebrates in the substratum (Tremblay and Magnan, 1991). In contrast, brook charr consume the largest benthic prey available both in sympatry and in allopatry, presumably because they select their prey one by one according to size. Therefore, the feeding behavior of white sucker leaves very few possibilities for brook charr to take competitive refuge on the benthic prey size axis (MacArthur and Levins. 1967; MacArthur, 1972; Roughgarden, 1974; Werner, 1977). It is probably for this reason that the white sucker has a greater impact than creek chub on the niche shift of brook charr from benthic to pelagic prey. In contrast to white sucker, gape-limitation in creek chub restricts it to a portion of the benthic prey size axis, which allows brook charr to feed on larger prey.

Two hypotheses, or a combination of both, could explain the decrease in the proportion of benthic specialists relative to that of pelagic ones in the presence of creek chub and white sucker. The first hypothesis is that benthic specialists shift to a pelagic diet, and thus to the pelagic form, somewhere in their ontogeny, following competition for benthic organisms of the littoral zone with chub and sucker. The mechanism underlying this shift would be phenotypic plasticity of individuals in response to the low profitability of the littoral zone in the presence of introduced species, through a reaction norm (i.e. the set of phenotypes that a given gene will express in response to different environmental conditions; Stearns, 1992). This would imply that the changes in morphology (pectoral fins) and coloration, observed by Bourke *et al.* (1997) could be induced within the lifetime of an individual. It has been shown experimentally that change in food type can induce, within a few months, consistent changes in trophic morphology in sunfish, cichlid, and stickleback species (Meyer, 1987; Wainwright *et al.*, 1991; Day *et al.*, 1993; Wimberger, 1994). In this context, the proportion of each form could conform to an Ideal Free Distribution, integrating both the intensity of competition (intra- and interspecific) and individual differences in foraging ability (Fretwell and Lucas, 1970; Parker and Sutherland, 1986). The second hypothesis is that the two forms are genetically distinct and that their abundance is mediated by different rates of mortality in littoral and pelagic zones. In allopatry, mortality could be solely a function of carrying capacity of each habitat (intraspecific competition component) while in sympatry, mortality would also be a function of competition with chub and sucker for benthic invertebrates of the littoral zone (intraspecific and interspecific competition components). In a comparison of 5 brook charr lakes and 5 brook charr and white sucker lakes, we found that mortality of young-of-the-year (YOY) brook charr is a function of interspecific competition: YOY charr were 93% less abundant (catch per unit of effort) in sympatry with white sucker than in allopatry ($p < 0.005$), (Venne and Magnan, 1995). Most of this mortality may be concentrated on benthic specialists, thus explaining their lower abundance in sympatry. Bourke *et al.* (1997) also provided some evidence of reproductive isolation between benthic and littoral individuals, using radio-telemetry: at the beginning of the 1992 spawning season, four of the nine tracked individuals moved among the three identified spawning grounds before finally selecting one. At the end of this spawning season, the four pelagic individuals were found in one inlet, the only benthic individual in another inlet, while three generalists were distributed in the three inlets. The results of O'Connor and Power (1973) also support the hypothesis of homing in brook charr, in one lake containing two spawning grounds. In this context, differences between the two forms could be maintained by disruptive selection, based on differential trophic efficiencies of individuals in littoral and pelagic zones. It is noteworthy that the proportion of generalists is low ($\sim$35%) and consistently similar among communities (Fig. 1). This result supports the hypothesis that natural selection does not promote intermediate forms because they have lower fitness than specialized ones (Schluter, 1994, 1995). The proportion of generalists could in fact be less than 35%; this value was obtained by subtracting from one the proportion of specialists, which is based on a conservative criterion (we considered that fish having >90% of a given prey type in their stomach were specialists on this prey type; benthic or pelagic specialists).

Although the two above mechanisms should be exclusive at any given time, they could both be involved over an evolutionary time scale; food segregation in response to intraspecific competition should occur first, through behavioral flexibility of individuals (changes in behavior being more flexible than changes in morphology and life history characters) → followed by development of specialized trophic morphology → followed by reproductive isolation (promoted by the use of different niches) → followed by genetic differentiation (see discussion by Wimberger, 1994; Skulason and Smith, 1995).

In conclusion, the relationship between interindividual variation in diet and individual variation in habitat use of brook charr is supported by different observations: (1) the analyses of diet were based on 3776 individuals distributed over 69 lakes, seven years, four summer months, and thus should be representative of a general pattern, (2) in allopatry, the proportion of benthic, pelagic, and generalist individuals inferred from diet in the present study fits remarkably well with that based on spatial distribution, identified through radio-telemetry during summer periods lasting 2–3 month in two lakes of the same system (Bourke *et al.*, 1997) and (3) individual specialization in habitat use was supported by functional relationships between habitat use and morphological traits such as pectoral fin length and coloration pattern (Bourke *et al.*, 1997). The results of the present study thus suggest that the pattern of interindividual variations in diet is representative of long term interindividual preferences in habitat use of brook charr. Furthermore, in addition to providing a strong field support to the current hypothesis that polymorphism is promoted by a relaxation of interspecific competition (Robinson and Wilson, 1994; Skulason and Smith, 1995), our results also indicate that phenotypic response of brook charr (i.e. the proportion of each form in a given lake) is related to the intensity of this competition.

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